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A biomechanical theory of inactivation

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1. Introduction

An important question in the literature focusing on motor control is to determine which laws drive biological limb movements. This question has prompted numerous investigations analysing arm movements in both humans and monkeys. Many theories assume that among all possible movements the one actually performed satisfies an optimality criterion (Todorov 2004). In the framework of optimal control theory, a first approach is to choose a cost function and test whether the proposed model fits with experimental data. A second approach (generally considered as the more difficult) is to infer the cost function from behavioural data. The cost proposed in this study includes a term called the absolute work of forces, reflecting the mechanical energy expenditure. Contrary to most investigations studying optimality principles of arm movements which used smooth cost functions [i.e. that have continuous derivatives up to some desired order, like the minimum jerk (Flash and Hogan 1985) or minimum torque change (Uno et al. 1989) models], the present model has the particularity of using a cost function that is not smooth. We have demonstrated in Berret et al. (2008) that under these assumptions agonistic and antagonistic muscles are inactivated during overlapping periods of time, for quick enough movements. Moreover, it has been shown that only this type of criterion can predict these inactivation periods. Finally, experimental evidence is in agreement with the predictions of the model. Indeed, we have checked the existence of simultaneous inactivation of opposing muscles during fast vertical arm movements.

2. Methods

For actuated mechanical systems, the physical quantity that measures energy is the work of forces. However, the work of a force pulling in the direction arbitrarily defined as positive may cancel with the work of the force pulling in the opposite direction. Therefore, work has to be always counted positive in order to express the energy expenditure

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ISSN 1025-5842 print/ISSN 1476-8259 online © 2009 Taylor & Francis DOI: 10.1080/10255840903065340 http://www.informaworld.com of a movement: this is the absolute work of forces. Indeed, the work of both the agonistic and antagonistic muscles requires a consumption of energy, provided by the hydrolysis of ATP to ADP, a physiological process taking place in muscle cells.

In this study, we consider arm movements around the shoulder joint in the sagittal plane (see Figure 1) whose dynamics is

$$J\ddot{\theta} = u - mglx\cos\theta.$$

Finding the motor strategies minimising such an energetic performance criterion is an interesting mathematical challenge. Here, we propose to minimise a compromise between the absolute work and the energy of acceleration in the sense of signal processing:

$$\int_0^T |u\dot{\theta}| + \alpha \ddot{\theta}^2 \mathrm{d}t \to \min_u.$$

This problem is solved using Pontryagin's maximum principle (and Clarke's non-smooth version).

In addition to the theoretical modelling, we also asked subjects to perform fast arm movements in the sagittal plane and measured both the kinematics of relevant anatomical points (shoulder, elbow, wrist, finger) and the EMG of the main muscles acting at the shoulder joint (deltoids, biceps, triceps).

A comparison between the model predictions and the experimental measurements has been used to assess the validity of the proposed cost function.

Before going further, let us define the term inactivation that is important in this study. An *inactivation* is the occurrence during a certain strictly positive time interval of an optimal trajectory corresponding to u = 0.

3. Results and discussion

Within this framework, we have the following mathematical principle: minimising a cost containing the absolute

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Figure 1. Illustration of the motor task (rotation around the shoulder joint) and of the arm's model. Variable u is the torque generated by muscles' action.

work implies the presence of stable inactivation in all nontrivial pointing movements for quick enough movements.

In other words, for a single-joint arm rotating around the shoulder joint, the minimum absolute work model predicts the existence of a time interval such that the net torque produced by muscles at the shoulder level is zero (see Figure 2(a)). During this period, only gravity is acting on the arm and it is in free-fall (if we neglect friction forces). This principle extends to more general cases where the agonist and antagonist actions of muscles are considered: both of them are zero during the inactivation interval. This model makes a fully testable and very singular prediction. Simultaneous periods of low-level muscle activities should be detected in the EMG of fast pointing arm movements. Interestingly, a reciprocal question is whether inactivation could be predicted by other kinds of cost functions, notably by smooth cost functions.

In answer to this question, the following proposition holds: if some optimal trajectories contain inactivation, then the cost function cannot be smooth with respect to u at u = 0.

Basically, a typical non-smoothness is of type 'absolute value function', but this could be more complicated. Nevertheless, taken together, these results show that the existence of inactivation is a sort of *necessary and sufficient condition* for the minimisation of a cost based on the absolute work of forces.

Due to the importance of the inactivation phenomenon, the experimental analysis was mainly focused on it. It appeared that the activity of the deltoids, biceps and triceps



Figure 2. Inactivation phenomenon for a fast upward arm movement: (a) model prediction and (b) experimental measurements.

was drastically decreased near the peak of velocity, showing the existence of very well-synchronised periods during which the main muscles acting at the shoulder joint are quasi-inactive (see Figure 2(b)). This is in agreement with the model prediction, and therefore gives evidence that a cost function similar to the absolute work (i.e. non-smooth at u = 0) is used by the brain to plan its movements.

4. Conclusions

In conclusion, from a methodological point of view, the novelty of the present work is to establish a necessary and sufficient condition to identify the cost function used by the brain to plan its movements. The possible existence of the inactivation phenomenon was deduced from a mathematical analysis and then checked experimentally. This study gives evidence for the integration of energetic considerations in human behaviour.

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